1999

Age, Growth, Longevity, And Mortality Of Blackcheek Tonguefish, Symphurus Plagiusa (Cynoglossidae : Pleuronectiformes), In Chesapeake Bay, Virginia

Mark R. Terwilliger
Virginia Institute of Marine Science

Thomas A. Munroe

Abstract.—Age structure, longevity, and mortality were determined for a population of blackcheek tonguefish, *Symphurus plagiusa*, in Chesapeake Bay. Blackcheek tonguefish (36–202 mm TL) were randomly collected by means of otter trawl in lower Chesapeake Bay and major Virginia tributaries (James, York, and Rappahannock rivers) from April 1994 through August 1995. Ages were determined by interpreting growth increments on thin transverse sections of sagittal otoliths. Marginal increment analysis showed that a single annulus was formed in June of each year. Blackcheek tonguefish caught during this study reached a maximum age of 5+ years. Growth was rapid during the first year, then slowed rapidly at a time coincident with maturation. We used the following von Bertalanffy growth equations: for males—$L_t = 196.5(1 - e^{-0.285(t + 0.92)})$; and for females—$L_t = 190.6(1 - e^{-0.320(t + 0.78)})$. Von Bertalanffy parameters were not significantly different between sexes. Extrapolated instantaneous mortality rates for a possible seventh year class were 0.73 (Hoenig's equation) and 0.77 (Royce's equation). High estimates of instantaneous total mortality may reflect either loss due to emigration of adults from Chesapeake Bay onto the continental shelf or high natural mortality occurring in this northernmost population. Compared with sympatric pleuronectiforms, blackcheek tonguefish have a relatively high mortality rate, small asymptotic length, and high growth parameter *K*. Species, such as blackcheek tonguefish, that feature this combination of growth parameters are hypothesized to be better adapted at exploiting seasonally dynamic and highly unpredictable environments, such as those estuarine habitats within Chesapeake Bay.

Manuscript accepted 15 June 1998.
Fish. Bull. 97:340–361 (1999).

Age, growth, longevity, and mortality of blackcheek tonguefish, *Symphurus plagiusa* (Cynoglossidae: Pleuronectiformes), in Chesapeake Bay, Virginia*

Mark R. Terwilliger
School of Marine Science, Virginia Institute of Marine Science
College of William and Mary
Gloucester Point, Virginia 23062
Present address: 104 Nash Hall
Department of Fisheries and Wildlife
Oregon State University
Corvallis, Oregon 97331
E-mail address: terwillm@ucs.orst.edu

Thomas A. Munroe
National Marine Fisheries Service National Systematics Laboratory, MRC-153
National Museum of Natural History
Washington, D.C. 20560

The blackcheek tonguefish, *Symphurus plagiusa* (Linnaeus, 1766), ranges from Connecticut southward through the Florida Keys, northern Gulf of Mexico, Cuba, and the Bahamas (Ginsburg, 1951; Topp and Hoff, 1972; Munroe, 1998). Chesapeake Bay is the northernmost location of a major population of this species (Munroe, 1998). South of Chesapeake Bay, blackcheek tonguefishes are an abundant component of the fish fauna occurring in estuaries and inshore coastal waters. Within this region, they occur in sufficient numbers to form a minor component of the bycatch of demersal fisheries and also constitute a minor inclusion in landings reported for several industrial fisheries. In the shrimp trawl fishery, they are a potential nuisance because individuals frequently become embedded in the webbing of trawls to such an extent that they interfere with the gear's effectiveness (Topp and Hoff, 1972).

The blackcheek tonguefish is the only member of the pleuronectiform family Cynoglossidae occurring in Chesapeake Bay (Ginsburg, 1951; Murdy et al., 1997; Munroe, 1998). This species is among the top three most abundant pleuronectiforms occurring throughout lower Chesapeake Bay and its tributaries (Bonzek et al., 1993; Geer et al., 1997). Only the hogchoker, *Trinectes maculatus*, is commonly taken in greater abundance in bottom trawls made within the Bay. Occurrence of all life history stages in Chesapeake Bay (Olney and Grant, 1976; Terwilliger, 1996) suggests that blackcheek tonguefish is a resident species in this system.

Despite its abundance in different estuarine and nearshore marine habitats in the northwest Atlantic, life history parameters of *S. plagiusa* are largely unknown. Some previous works have described distribution, relative abundances and length frequencies for blackcheek tonguefish in South Carolina estuaries (Shealy et al., 1974); some have summarized size-related maturity patterns for individuals from throughout the entire range of the species (Munroe, 1998); some have

* Contribution 2203 of the Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062.

investigated factors influencing recruitment (Miller et al., 1991); and some have described daily growth rates of juveniles in Georgia estuaries (Reichert and van der Veer, 1991). The minimal amount of published information on this species (summarized in Munroe, 1998) may be due in part to the relatively small size of the fish. It reaches a maximum size of approximately 210 mm total length (TL) (Wenner and Sedberry, 1989), but fish smaller than 165 mm TL are those most commonly taken in Chesapeake Bay by otter trawl (Terwilliger, 1996; Geer et al., 1997). Small size and benthic microinvertebrate feeding habits (Stickney, 1976; Reichert and van der Veer, 1991; Toepfer and Fleeger, 1995) render this species inaccessible to most recreational and commercial fishing gears used in Chesapeake Bay.

Few age and growth studies using bony structures or otoliths exist for species of the Cynoglossidae. This relatively large gap in knowledge for approximately 150 species of tonguefishes was recently noted in a compilation of flatfish life history parameters (Miller et al., 1991). Although several studies have described growth for species of *Cynoglossus* from the eastern Atlantic (Chauvet, 1972), western Pacific (Lin, 1982; Meng and Ren, 1988; Zhu and Ma, 1992), and Indian Ocean (Seshappa, 1976, 1978, 1981; Ramanathan et al., 1980; Seshappa and Chakrapani, 1984), no growth studies using bony structures or otoliths have been performed on species of *Symphurus*. Previous work describing the age structure of blackcheek tonguefish in Chesapeake Bay using length frequencies of fish taken by otter trawl (Bonzek et al., 1993) is limited because this type of analysis requires subjective interpretation of modal frequencies in the data, which, given the difficulty of distinguishing modal groups at older ages, renders the interpretation unreliable (Chauvet, 1972; White and Chittenden, 1977; Jearld, 1983; Barbieri, 1993). Such limitations in interpretation of age from length-frequency distributions are particularly evident in data from Koski's (1978) study on hogchokers from the Hudson River estuary, where the first of bimodal peaks in a frequency distribution of hogchoker lengths corresponded to age-1 fish, whereas the second peak represented combinations of length distributions for fishes age 2–6 yr. Chauvet's (1972) data for *C. canariensis* off West Africa also show a similar pattern of overlapping sizes among fishes of different ages.

Symphurus plagiusa is a good candidate for an age and growth study. It is unique among the Cynoglossidae in that it is the only species of this family that inhabits estuarine environments in the seasonally dynamic region of north temperate latitudes. Most other cynoglossid species occur in the tropics and are difficult to age from hard parts because environmental constancy precludes the formation of interpretable annular growth marks on these structures (Qasim, 1973). Other species of symphurine tonguefishes that occur in temperate waters generally are small-size, deep-water forms that are difficult to catch in abundance (Munroe, 1998).

This study was undertaken to determine age structure, growth rate, longevity, and mortality for a population of *S. plagiusa* residing in Chesapeake Bay, Virginia. Knowledge about life history parameters for this species provides a window of understanding into the biology of the Cynoglossidae, as well as insights into age, growth, and longevity of other small-size, estuarine-dependent flatfishes.

Materials and methods

Blackcheek tonguefishes were collected by 9.14-m semiballoon otter trawl with a 38.10-mm stretch mesh body, 6.35-mm mesh codend liner, and attached tickler chain (Bonzek et al., 1993). Fish were collected from April 1994 through August 1995 during the Virginia Institute of Marine Science (VIMS) Juvenile Finfish and Blue Crab Stock Assessment Program's trawl survey. The survey employs a monthly, random-stratified design of the lower Chesapeake Bay and fixed-station mid-channel transects in each of three major Virginia tributaries: the York, James, and Rappahannock rivers (Fig. 1). Details of sampling design were provided in Geer et al. (1993).

Samples of blackcheek tonguefishes selected from trawl catches were brought to the laboratory, measured for total length (TL) to the nearest millimeter and for total weight (TW) taken to the nearest hundredth of a gram. When samples were small, all fish were used in age analyses; however, fish were randomly selected for age analyses from relatively large samples. Regressions were fitted to the length–weight data, and regressions on log-transformed data for male and female blackcheek tonguefish were compared by using analysis of covariance (ANCOVA). The formula to convert SL to TL for blackcheek tonguefish provided by Jorgenson and Miller (1968:11) was used when comparing length data (reported as SL) from other studies.

All fish were sexed macroscopically, and then gonads were removed and preserved for later histological analysis to determine maturity stages (Terwilliger, 1996). Males were classified as either immature or mature according to the absence or presence of spermatozoa in the testes; females were considered mature if they showed any evidence of developing oocytes or previous spawning, e.g. thickening of the ovarian membrane.

Both sagittal otoliths were removed, cleaned, and stored dry for later processing. Otolith maximum

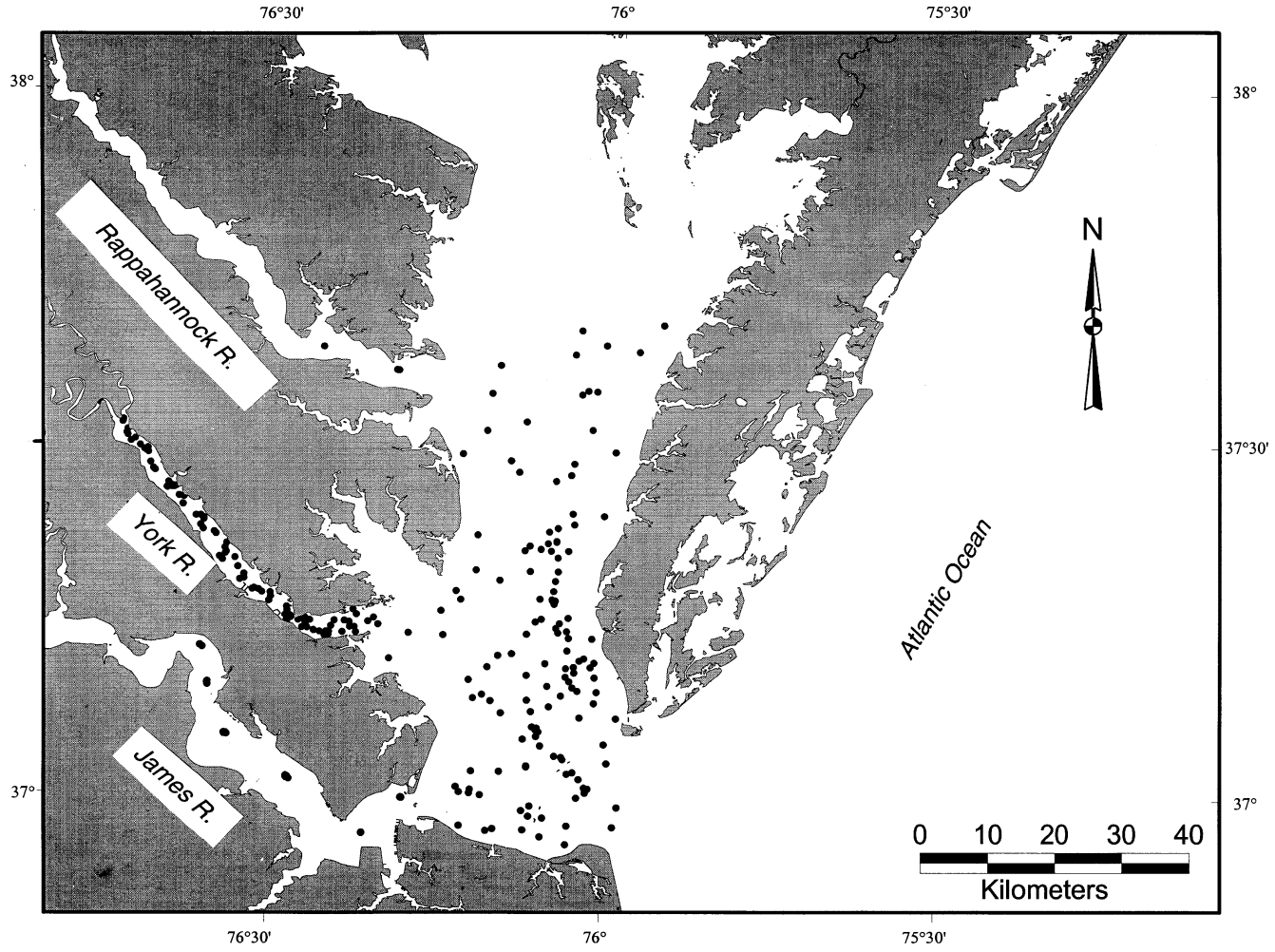

Figure 1

Lower Chesapeake Bay system, including James, York, and Rappahannock rivers. Points indicate stations where blackcheek tonguefish, *Symphurus plagiusa*, were collected, April 1994–August 1995.

diameter (distance from anterior tip of rostrum to postrostrum) was measured to the nearest 0.00001 mm by using a compound microscope coupled with a video camera interfaced with a microcomputer equipped with Biosonics' Optical Pattern Recognition System (OPRS) software (Biosonics, Inc., 1987). Because no asymmetry in otolith shape was apparent, sagittal otoliths (left or right) were arbitrarily selected from each fish for age analysis, embedded in epoxy resin (Spurr, 1969), and sectioned transversely (1 mm thick) through the core with a Buehler Isomet low-speed saw with duel diamond blades. Sections were mounted on glass slides with Crystal Bond adhesive, sanded with 1000-grit sandpaper to remove saw marks and to gain proximity to the core, polished with alumina powder, and examined with a binocular dissecting microscope (30×) with transmitted light and bright field. Annuli on otoliths from all 566 blackcheek tonguefish were counted once a month for three months. Counts were made without information regarding fish length or catch date. In 185 (32.7%) cases, the first and second readings did not agree and a third reading was made. The majority of disagreements in age estimates occurred during the beginning of the study; subsequent re-ageing resolved most discrepancies in age estimates. In most cases, the second reading of an otolith section differed from the first reading by only one year. If a third reading agreed with either of the first two, then that age was assigned to the otolith. In 28 (5%) cases, the third reading was different than the first and second readings. These 28 otoliths were considered unreadable and excluded from further analysis.

Otolith annuli were validated by the marginal increment method (Bagenal and Tesch, 1978; Jearld, 1983). Distances from the core to each annulus and the proximal edge were computed by drawing a vertical line from the core to the proximal edge of the

otolith with the OPRS. The average margin width, i.e. the translucent region between the last annulus and the proximal edge of the otolith, was plotted by month.

Regression analyses of otolith maximum diameter on total length and of weight on total length were calculated by the method of least squares. Back-calculated lengths-at-age were computed by using the Lee method (Lagler, 1956). To evaluate growth, back-calculated lengths-at-ages were fitted to the von Bertalanffy model (Ricker, 1975) by using nonlinear regression (Marquardt method) calculated with Fishparm computer software (Saila et al., 1988). Likelihood-ratio tests were used to compare parameter estimates of the von Bertalanffy equation for males and females (Kimura, 1980; Cerrato, 1990).

A scale sample from a region in the posterior third of the body, dorsal to the midline, was taken from all fish. Six scales from each fish were cleaned with hydrogen peroxide and mounted on plastic strips by using a Carver hydraulic laboratory press. A random sample of scale strips from 50 fish were then viewed with a microfiche reader in order to discern annuli for comparison with otolith sections. In contrast to otoliths, scales proved to be unreliable for ageing this species. Annuli were poorly defined and difficult to distinguish, and in many cases, the scales were unreadable. Fish ages obtained from scales agreed with ages obtained from otoliths in only 12% of the cases. This is not surprising, because scale annuli from other fish species with known ages have been shown to be inconsistent indicators of age, even in relatively young fish (Prather, 1967; Heidinger and Clodfelter, 1987).

Instantaneous total annual mortality rates, Z, were estimated from maximum age estimates with a pooled regression equation as suggested by Hoenig (1983) and by calculating a theoretical total mortality for the entire lifespan following the reasoning of Royce (1972) as described in Chittenden and McEachran (1976). Values of Z were converted to total annual mortality rates, A, using the relationship $A = 1 - e^{-Z}$ (Ricker, 1975).

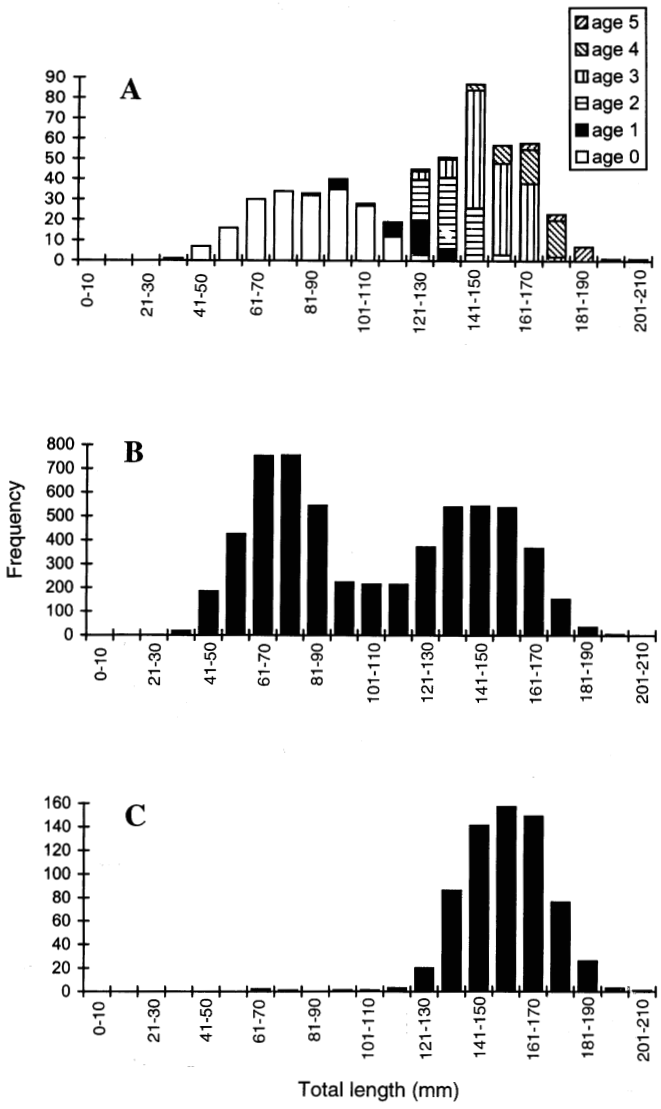

Figure 2

Length-frequency distribution for blackcheek tonguefish, *Symphurus plagiusa*: (**A**) length frequency for blackcheek tonguefish from lower Chesapeake Bay and major lower tributaries for fishes aged in this study; (**B**) length frequency for blackcheek tonguefish caught by Virginia Institute of Marine Science's juvenile fish recruitment trawl survey in lower Chesapeake Bay and major lower tributaries, 1993–1996; (**C**) length frequency for blackcheek tonguefish caught at the mouth of Chesapeake Bay and inner shelf off Virginia and North Carolina, 1987–89.

Results

A total of 566 fish, encompassing a size range from 36 to 202 mm TL (Fig. 2A), were used in this ageing study. This size range included individuals from all life history stages from postsettling juveniles to mature adults. The sex ratio for blackcheek tonguefish collected in this study was 223 males:343 females, or 1:1.54. A G-test of the sex ratio for 566 blackcheek tonguefish indicated statistically significant deviations (G=25.64; df=1; P<0.001) from a 1:1 sex ratio (Table 1). A G-test of sex ratios for blackcheek

Table 1

G-test of sex ratio for blackcheek tonguefish, *Symphurus plagiusa*, caught in lower Chesapeake Bay and three Virginia tributaries, April 1994–August 1995 (**A**) total catch; (**B**) by 25 mm size increment. Yates' correction for continuity implemented in (**B**) due to small sample sizes. *n* = number of fish; df = degrees of freedom; ns = nonsignificant.

A

	Males	Females	*n*	df	*G*	*P*
Frequency	223	343	566	1	25.64	10.83*
Expected	283	283				

* $P<0.001$.

B

Length	Males	Females	*n*	df	*G*	*P*
26–50	7.5	4.5	12	1	0.7580146	ns
Expected	6.0	6.0				
51–75	18.5	36.5	55	1	6.0008514	5.024**
Expected	27.5	27.5				
76–100	46.5	53.5	100	1	0.4904009	ns
Expected	50.0	50.0				
101–125	26.5	44.5	71	1	4.6135656	3.841*
Expected	35.5	35.5				
126–150	68.5	106.5	175	1	8.3175269	7.879***
Expected	87.5	87.5				
151–175	51.5	91.5	143	1	11.339487	10.828****
Expected	71.5	71.5				
176–200	7.5	8.5	16	1	0.0625408	ns
Expected	8.0	8.0				
201–225	0.5	1.5	2	1	0.5232481	ns
Expected	1.0	1.0				

* $P<0.05$; **$P<0.025$; ***$P<0.005$; ****$P<0.001$.

tonguefish broken down into 25-mm length increments showed that females dominated many intermediate size classes (Table 1).

The length–weight relationships for 200 males (48–190 mm TL) and 310 females (46–202 mm TL) (Fig. 3) were

$$\text{Males:} \quad W = 10^{-5.30}\,(TL^{3.126});$$
$$\text{Females:} \quad W = 10^{-5.37}\,(TL^{3.163}).$$

No statistically significant differences were found between sexes in the total length-total weight relationships (ANCOVA; F=3.86; df=506; P>0.25). The length-weight relationship for sexes combined was

$$W = 10^{-5.34}\,(TL^{3.148}).$$

Size at sexual maturity observed in female and male blackcheek tonguefish ranged between 80–130 mm TL and 70–110 mm TL, respectively. Length at which 50% of the population reached maturity was 101 mm TL for females and 91 mm TL for males (Fig. 4).

Sagittal otoliths of blackcheek tonguefish are small, round, dense structures that cannot be read whole. Transverse sections of otoliths (Fig. 5), however, revealed fairly distinct opaque bands that could be counted. Transverse sections through otoliths indicated that otolith structure consists of an opaque core usually surrounded by a wide opaque area whose outer edge demarcates the first annulus. Size and appearance of this first annulus vary among fish, ranging from a broad band continuous with the core to a narrow opaque band not continuous with the core. Subsequent annuli are represented by thin opaque bands encircling the core and by broader translucent zones found between annuli. At the margin of the otolith, an annulus was difficult to observe. However, when sufficient spring and early summer growth had occurred and contributed translucent material to the margin of the otolith after annulus

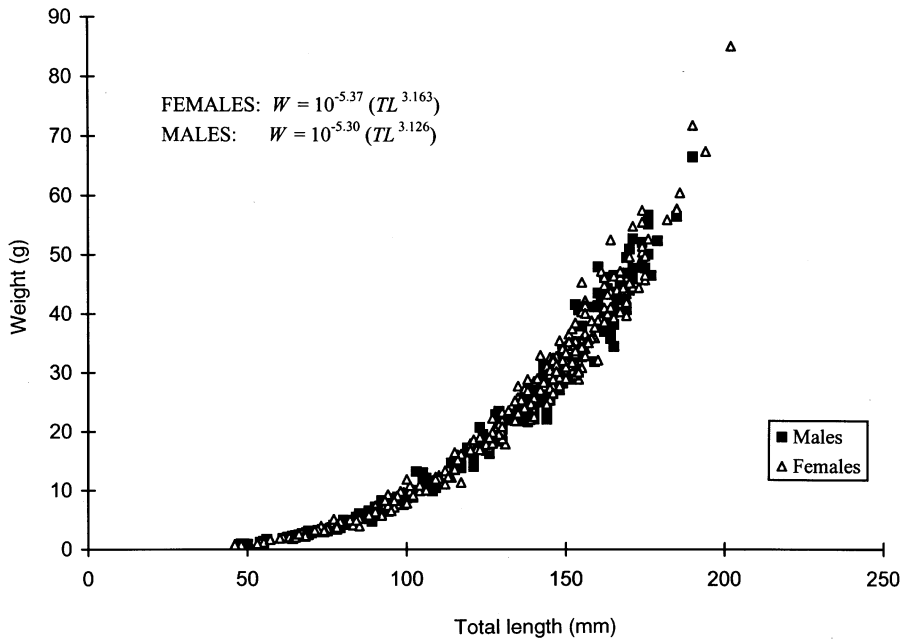

Figure 3

Total length–weight relationship for both sexes of blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries.

formation, the densely compacted opaque zone delimiting the annulus was easily identifiable. The combination of one broad translucent zone and one narrow opaque zone (Fig. 5) represents one year's growth.

Otolith maximum diameter (OMD) was linearly related to total length (Fig. 6) and described by the following relationship:

$$TL = 64.59(OMD) - 17.02. \qquad [r^2=0.93]$$

This linear relationship indicated that otolith growth was proportional to fish growth.

Size at first annulus formation for blackcheek tonguefish ranged from 88 to 138 mm TL (mean length ca. 118 mm TL). Seasonal progression of modal length frequencies (Fig. 7) for young-of-the-year fish (YOY) corroborated first-year growth-rate estimates determined from annular marks on the otoliths. Pooled data for 1993–96 from VIMS[1] trawl survey reports indicated that YOY blackcheek tonguefish recruited to the gear during September, usually at sizes of ca. 35–45 mm TL. By the following June, these fish had reached sizes ranging from ca. 53 to 138 mm TL. Thus, empirical data from length frequencies agreed fairly well with first-year growth estimates derived from interpretation of annulus formation on the otoliths.

Monthly mean marginal increments on the otoliths were plotted for fish from all age groups (Fig. 8). The seasonal progression of marginal increments was similar on otoliths from all age groups; therefore, data were pooled to demonstrate general trends in annual growth. Marginal increments were smallest during June of both 1994 and 1995. Monthly mean marginal increments showed only one trough during a year, indicating that a single annulus is formed yearly in June. In 1994, margin width on the otoliths increased rapidly during July and August, reflecting an active period of growth. After August 1994, margin width leveled off and remained fairly constant from September 1994 through May 1995. Large variation (indicated by high standard error) for samples taken during May of both 1994 and 1995 may indicate that the season of annulus formation may be somewhat more protracted (May–June) and perhaps dependent upon environmental factors. Alternatively, it may simply reflect an artifact of the small sample sizes examined from this period.

Mean lengths at age were backcalculated for 92 males and 145 females (Table 2). Remaining fish were young-of-the-year and therefore were excluded from this analysis. Observed (empirical) lengths were con-

[1] VIMS (Virginia Institute of Marine Science), Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

sistently higher than the back-calculated lengths-at-age for individual age groups, which indicated that seasonal growth had occurred since formation of a new annulus. Differences between back-calculated lengths-at-age and observed lengths are in the range of observed seasonal growth. Males and females have similar lengths-at-age until age 4 (Table 2). Beyond age 4, mean lengths for females were slightly greater than those for males. The largest male collected in this study was 190 mm (age 5+); the largest female collected was 202 mm (age 5+).

Greatest incremental growth in TL for both sexes occurred during the first year and then declined rapidly thereafter (Table 2). Mean back-calculated lengths for females and males at the end of their first year were 78.84 mm and 75.68 mm, respectively. Growth for both sexes in the second year was only 39–41% of that recorded for the first year. Growth increments continued to decrease every year thereafter for both sexes until age 5, when the estimated growth increment increased slightly for both sexes. This increase at age 5 may be an artifact due to the relatively small number of samples for both sexes in this age group.

Length frequency for blackcheek tonguefish caught by VIMS[2] trawl survey (1993–96) shows a bimodal distribution (Fig. 2B), but this distribution does not adequately reflect age composition of the individuals, especially for fishes larger than 110 mm TL. Despite the bimodal distribution in length frequencies, six age groups are represented in this distribution, and much overlap in total length exists between age groups, especially those consisting of medium- and large-size fish. These data indicate that length frequency analyses are unreliable age estimators for older individuals of this species.

Von Bertalanffy parameters were computed (Table 3) by using lengths backcalculated to the most recent annuli to reduce bias in asymptotic length and growth coefficient K due to the presence of Lee's phenomenon in the back-calculated lengths-at-age (Vaughan and Burton, 1994). The growth coefficient K for female blackcheek tonguefishes (0.320) was greater than that (0.285) calculated for males. Males and females achieved 50% of L_∞ by the end of their first year and 75% between ages 2 and 3 (Fig. 9). Results of likelihood-ratio tests (Table 4) showed no significant differences in the overall von Bertalanffy growth models for males and females (χ^2=6.56, df=3, P=0.09). Estimates of L_∞ (χ^2=0.10, df=1, P=0.75), K (χ^2=0.03, df=1, P=0.87), and t_0 (χ^2=0.19, df=1, P=0.67) were not significantly different between sexes.

Values for asymptotic lengths for both sexes agreed well with observed lengths. The largest male collected in this study was 190 mm and the calculated L_∞ for males was 196.5 mm. The largest female collected in this study was 202 mm and the calculated asymptotic length for females was 190.6 mm. These results are acceptable because asymptotic length is a regression estimate, and thus an average that represents an average maximum length if fish live and grow according to the von Bertalanffy equation. Nevertheless, the overall estimated asymptotic length value (192.4) represents a reasonable approximation of the average maximum length estimate for the species.

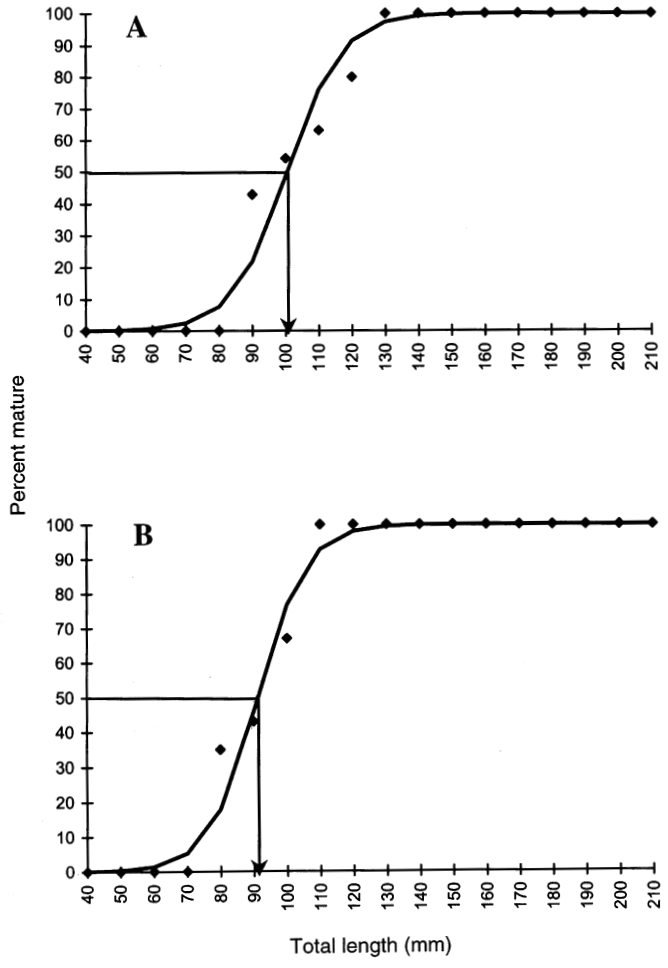

Figure 4

Length at maturity for blackcheek tonguefish, *Symphurus plagiusa*, in lower Chesapeake Bay and major lower tributaries: (**A**) females; (**B**) males. Arrow represents length at 50% maturity.

[2] VIMS, Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

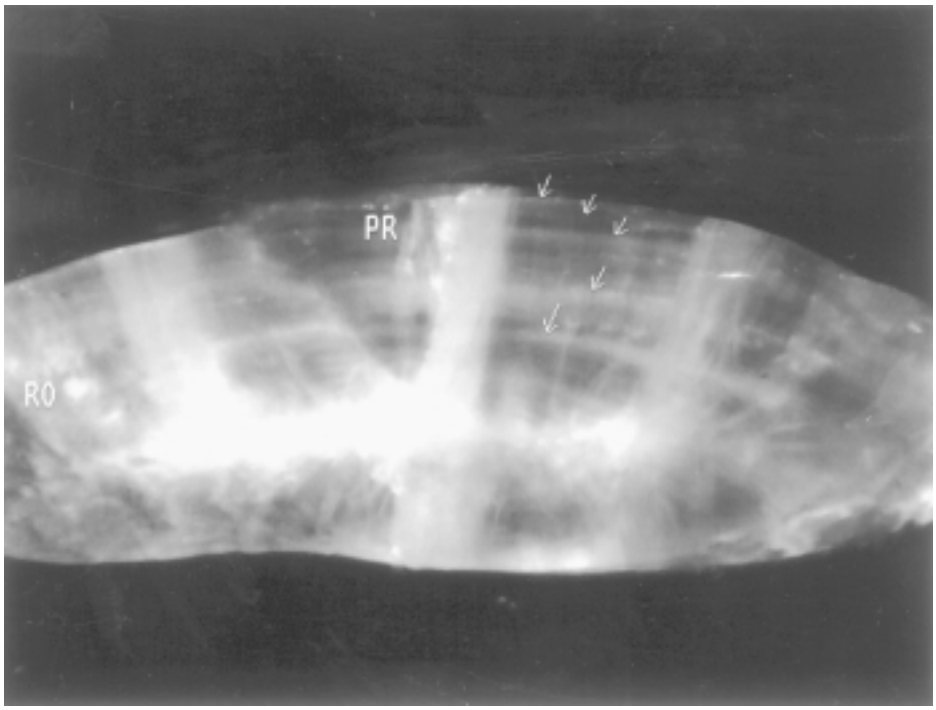

Figure 5

Transverse section from a sagittal otolith of a blackcheek tonguefish, *Symphurus plagiusa*, collected in lower Chesapeake Bay and major lower tributaries. Age 5+. Arrows indicate annuli. Pr = proximal; Ro = rostral.

Table 2

Mean observed and back-calculated lengths for female and male blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay: ages 1–5.

Age	Sample size	Size range (mm)	Mean observed length (mm)	Mean back-calculated lengths at successive annuli (mm)				
				I	II	III	IV	V
Females								
1	15	93–138	121.07	83.943				
2	31	127–155	136.81	81.156	115.272			
3	64	126–170	153.33	76.038	113.238	135.832		
4	25	135–175	161.62	70.073	101.826	126.549	145.385	
5	10	162–202	181.20	82.966	108.644	129.812	150.714	167.936
Mean length				78.835	109.745	130.731	148.049	167.936
Growth increment				78.835	30.910	20.986	17.318	19.887
Males								
1	12	88–125	115.83	81.778				
2	22	103–146	136.59	82.844	113.864			
3	31	130–171	154.19	76.573	110.408	133.553		
4	23	146–179	166.52	73.339	107.662	129.228	148.911	
5	4	162–190	177.75	63.838	95.125	118.058	141.277	163.721
Mean length				75.675	106.765	126.946	145.094	163.721
Growth increment				75.675	31.090	20.182	18.147	18.628

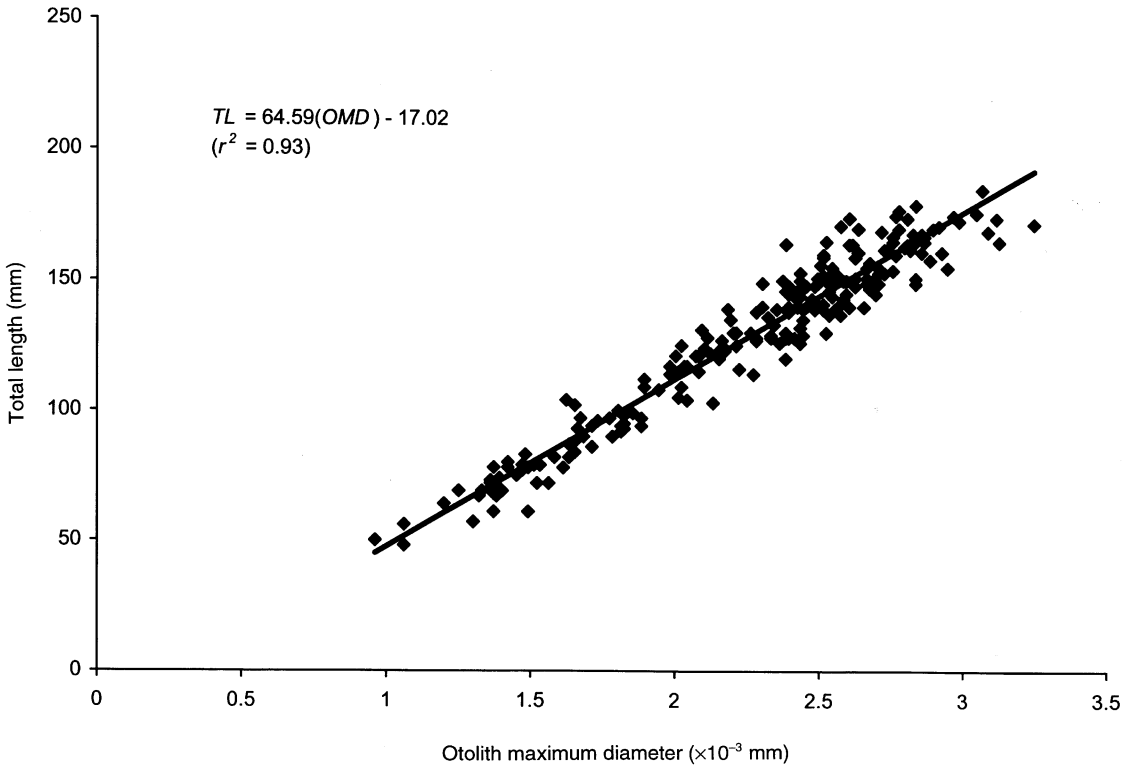

Figure 6

Linear regression of total length (mm) on otolith maximum diameter (mm) for blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries.

Instantaneous total mortality (Z) estimates obtained for a maximum age of 5 years were 0.87 (A=58%) with Hoenig's (1983) method, and 0.92 (A=60%) with Royce's (1972) method. A plot of age composition of the catch (Fig. 10) indicates rapidly declining numbers of fishes aged 4 and 5.

Discussion

Most of what we know regarding growth in cynoglossid flatfishes stems from information gathered from studies conducted on species of *Cynoglossus*. These are tonguefishes usually much larger in size than species of *Symphurus* (Menon, 1977), and species which also occur predominantly in the shallow tropical seas of the Indo-West Pacific. Therefore, the present study detailing information on age, growth, and longevity for blackcheek tonguefish is significant in being the first of its kind reporting such life history parameters for a member of *Symphurus*. Furthermore, of the approximately 150 species of Cynoglossidae, *S. plagiusa* is unique in that it is the only member of the family inhabiting temperate estuarine environments in the seasonally dynamic Chesapeake Bay region of the western North Atlantic. In fact, the tonguefishes inhabiting Chesapeake Bay are the northernmost major population of this species (Munroe, 1998). Here, the species has ranked as high as sixth in overall abundance, and in some years is the second most abundant pleuronectiform among fishes taken during trawling in lower Chesapeake Bay and its tributaries (Geer et al., 1993). North of the Chesapeake Bay region, adult blackcheek tonguefish are relatively rare (Munroe, 1998), even in such proximate estuaries as Delaware Bay. Just how long the Chesapeake Bay has supported a significant population of this species is unknown because earlier compilations on fishes of the region (Hildebrand and Schroeder, 1928) regarded this species as occurring only rarely within the Bay. It is conceivable that because of its relatively small size and benthic habits, the abundance of this species may have been grossly underestimated during previous fish surveys conducted in this region. However, given the general rarity of this species in areas immediately to the north, and the observed incidences of winter mortalities within Chesapeake Bay (see be-

Table 3

Von Bertalanffy parameters and equations calculated for male and female blackcheek tonguefish, *Symphurus plagiusa*, collected in Chesapeake Bay, Virginia. Values in parentheses are standard errors.

Parameter	Males	Females	Combined
K	0.285	0.320	0.308
	(0.075)	(0.061)	(0.047)
L_∞	196.5	190.6	192.4
	(20.04)	(13.03)	(10.88)
t_0	–0.920	–0.784	–0.832
	(0.289)	(0.216)	(0.172)
Equation	$L_t = 196.5\ (1 - e^{-0.285(t + 0.920)})$	$L_t = 190.6\ (1 - e^{-0.320(t + 0.784)})$	$L_t = 192.4\ (1 - e^{-0.308\ (t + 0.832)})$

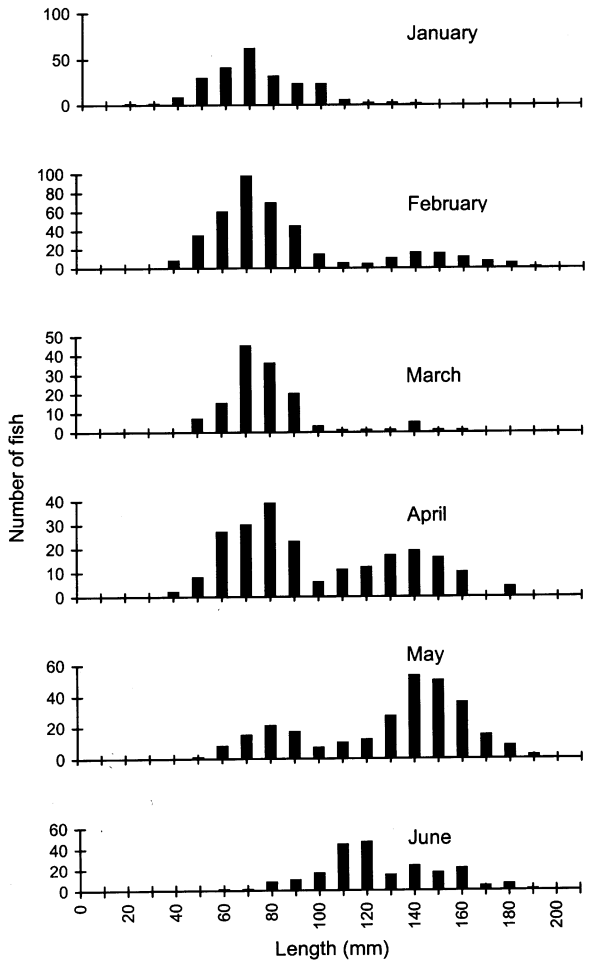

Figure 7

Seasonal progression of modal length frequencies for blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries, 1993–96.

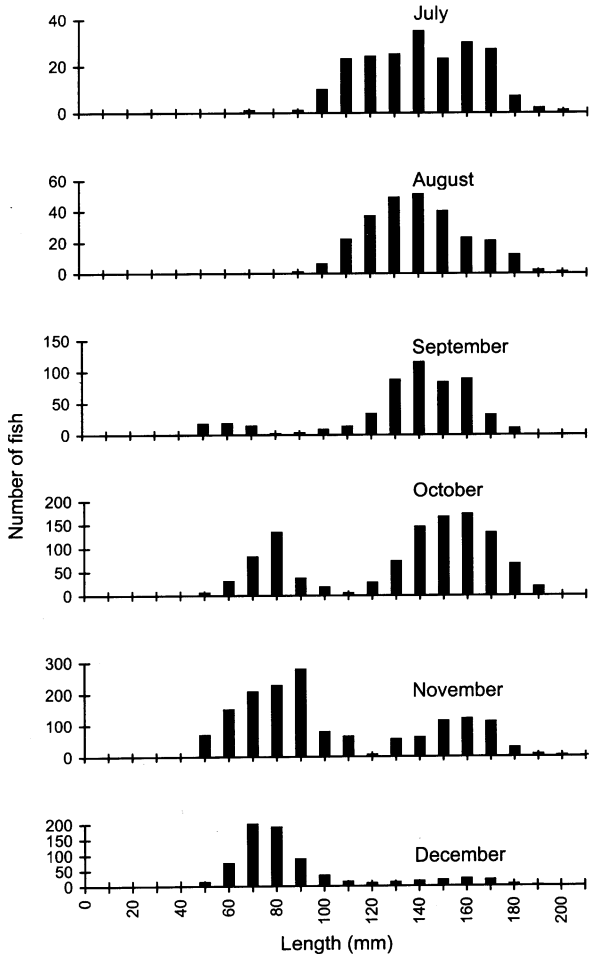

Figure 7 (continued)

low), it also seems equally possible that the population of blackcheek tonguefishes residing in Chesapeake Bay could be of more recent origin because all other major populations for this species are known to occur only in areas further to the south. If indeed this is the case, then life history parameters estimated for blackcheek tonguefishes from Chesapeake Bay are those characterizing a peripheral population of the species. Comparisons of these estimates

of life history parameters, then, with values derived from other, more centrally located, populations of this species, as well as with those from populations inhabiting subtropical environments in northern Mexico and Cuba (Munroe, 1998), would prove interesting from the perspective of discovering the range of variability in life history features that has evolved within this species of flatfish.

Sizes of blackcheek tonguefishes collected within Chesapeake Bay during the present study represent almost the complete size range known for the species (Munroe, 1998). The largest female (202 mm TL) and largest male (190 mm TL) taken within the Bay approach the largest sizes known for this species (ca. 210 mm TL; Wenner and Sedberry, 1989). However, most blackcheek tonguefishes occurring within this system were smaller, with total lengths usually ranging between 35 and 150 mm. The size range for blackcheek tonguefishes occurring in Chesapeake Bay is not unlike those reported for other estuarine populations located throughout the species' range. For example, Shealy et al. (1974) reported that, during a year-long survey of fish assemblages in South Carolina estuaries, blackcheek tonguefishes ranged in size from 53 to 156 mm TL. However, modal lengths for this species were never greater than 140 mm TL, and fish were usually much smaller (monthly mean size 97–124 mm TL). In fact, of the blackcheek tonguefishes taken during that study, only 8 of 362 (2.2%) were 150 mm TL or larger.

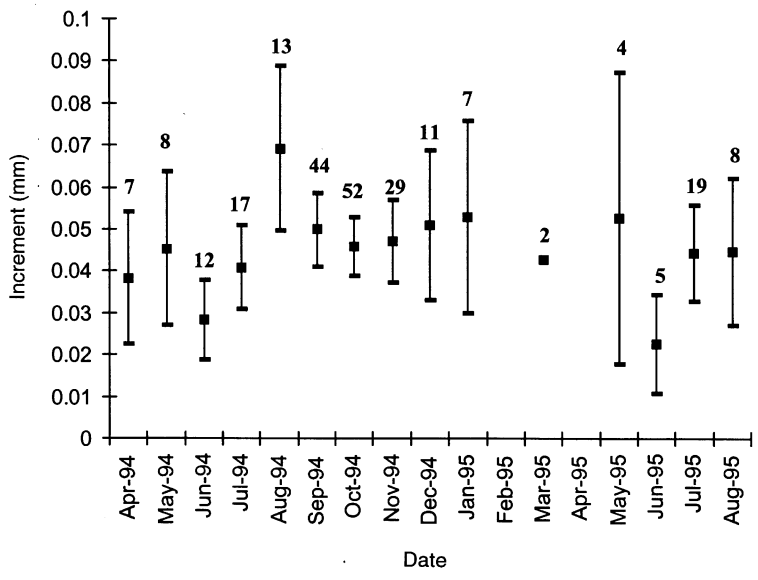

Figure 8

Plot of monthly mean marginal increments for blackcheek tonguefish, *Symphurus plagiusa*, ages 1–5, collected in lower Chesapeake Bay and major lower tributaries. Vertical bars represent ±1 standard error. Numbers above bars represent monthly sample sizes.

Although many studies (summarized in Munroe, 1998) have reported catching large blackcheek tonguefish from neritic habitats on the inner continental shelf throughout the species' range, size ranges for these fishes were not unlike those observed for blackcheek tonguefishes collected within Chesapeake Bay. For example, blackcheek tonguefishes (n=439) collected at the mouth of Chesapeake Bay and on the inner continental shelf off southern Virginia and northern North Carolina (VIMS[3]) during a series of cruises conducted during 1987–89 ranged from 68 to 203 mm TL (mean size= 154.5 mm TL; Fig. 2C); and most fishes

[3] VIMS, Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

Table 4

Likelihood ratio tests comparing von Bertalanffy parameter estimates for male (1) and female (2) blackcheek tonguefish, *Symphurus plagiusa*, from Chesapeake Bay, Virginia. df = degrees of freedom.

Hypothesis	Linear constraints	Residual SS	χ^2_r	df	P
HΩ	none	99,760.5			
Hω1	$L_{\infty 1} = L_{\infty 2}$	99,780.9	0.1043	1	0.7467
Hω2	$K_1 = K_2$	99,765.8	0.0271	1	0.8692
Hω3	$t_{01} = t_{02}$	99,796.9	0.1861	1	0.6661
Hω4	$L_{\infty 1} = L_{\infty 2}$	10,051.6	6.558	3	0.0874
	$K_1 = K_2$				
	$t_{01} = t_{02}$				

measured 140–180 mm TL. Lengths of fishes collected within the Bay system completely overlap those taken from the nearby shelf. Munroe (1998) noted that most blackcheek tonguefishes in collections from throughout the species' geographic range were usually much smaller than the largest sizes known for the species because only 4% of 568 fish he examined exceeded 164 mm TL. Wenner and Sedberry (1989) sampled 8780 blackcheek tonguefishes from coastal habitats (<10 m depth) between Cape Fear, North Carolina, and the St. Johns River, Florida, and reported that length composition of trawl-caught *S. plagiusa* was consistent from season to season, with mean sizes ranging between 140–150 mm TL. The largest specimens taken during that study were 210 mm TL, and few fish <100 mm TL were caught, possibly because fish smaller than this inhabited a different habitat as juveniles or because they did not recruit to the fishing gear until 100 mm TL. On the continental shelf off Tampa Bay, Florida, lengths (124–174 mm TL) for blackcheek tonguefishes were also similar to those reported for fish from Chesapeake Bay (Moe and Martin, 1965).

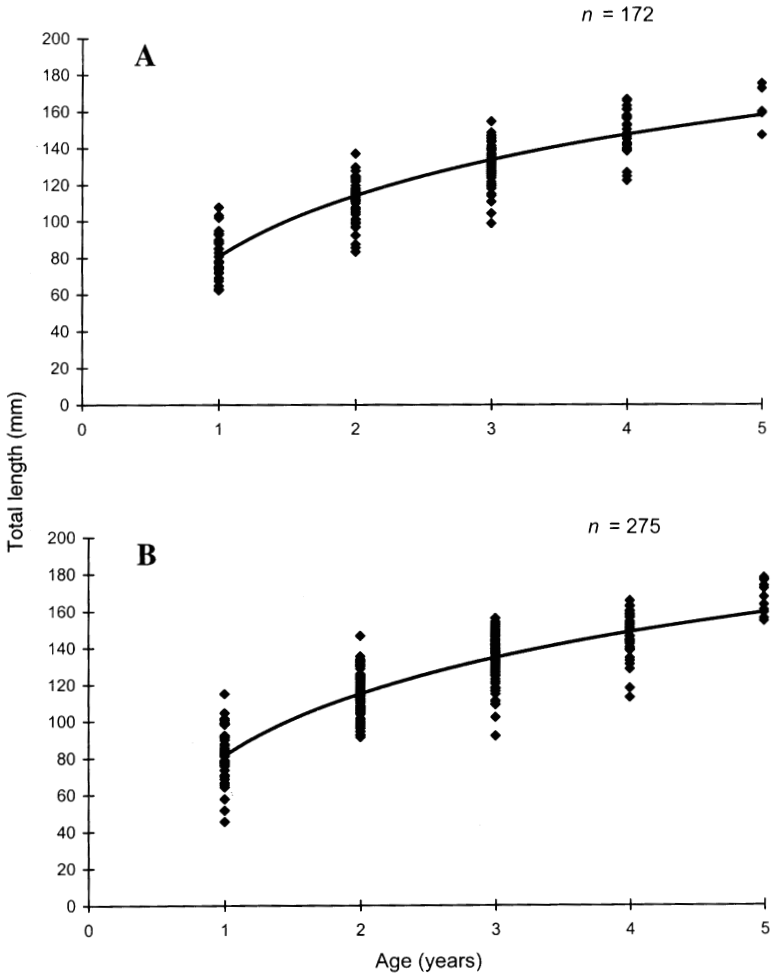

Figure 9

Plot of back-calculated and predicted lengths from the von Bertalanffy growth model for blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries: (**A**) males; (**B**) females.

Although age estimates are not available for other populations of blackcheek tonguefish, a general comparison of growth between blackcheek tonguefishes occurring in Chesapeake Bay with those from other areas is provided by examination of length–weight parameters derived for different populations. Dawson (1965) generated a length-weight relationship for 3504 blackcheek tonguefish (43–148 mm TL) occurring in Gulf of Mexico waters. With this relationship, weights were generated from 510 randomly selected lengths between 43 and 148 mm TL and these were then compared with a similar number of weights generated for fishes of the same size range by using the length-weight relationship derived for blackcheek tonguefishes from Chesapeake Bay. No significant differences (t=0.53; df=1010; P=0.60) were evident in this comparison between weights of fishes of these two regions, indicating that growth in weight, at least, is similar for fishes of this size range occurring in these widely separated areas within the species' range.

Annuli form on the otoliths of blackcheek tonguefishes from late spring through early summer (mostly June), coincident with the summer warming period and also at the initiation of the spawning season (Terwilliger, 1996). For *C. abbreviatus,* a tonguefish occurring in temperate seas off eastern China (Zhu and Ma, 1992), annuli form on otoliths during March–May, a period also corresponding to seasonal timing of gonad maturation and warming of water temperatures. Koski (1978) reported that annuli form on scales of hogchokers in the Hudson River from April to mid-June, which is a period of increasing water temperature, and for mature fish this also corresponds to the time just prior to and overlapping the early spawning season.

Flatfishes typically exhibit sexual dimorphism in size at age (Roff, 1982; and others, see below)—

females usually growing larger than males. In the Chesapeake Bay population, male and female blackcheek tonguefishes attain similar maximum sizes (mean value for oldest females=181.2 mm TL; mean value for oldest males=177.8 mm TL). In summarizing size information for blackcheek tonguefishes collected throughout the geographic range of the species, Munroe (1998) also reported no significant size differences between males (to 174 mm TL) and females (to 172 mm TL). For 23 other species of western Atlantic tonguefishes, females reached larger sizes than males in 11 of these species, in six others a larger size was reported for males, whereas in seven other species similar maximum sizes were attained by both sexes (Munroe, 1998). However, since no age estimates have been made for these other species of *Symphurus*, comparative data on dimorphism in lengths at age for these symphurine tonguefishes are unavailable. For other cynoglossids with accompanying age data, considerable variation exists in the degree of sexual dimorphism evident in sizes attained by the sexes. In the Malabar sole (*Cynoglossus semifasciatus*) off India, females grow larger than males, although reported differences in maximum sizes between sexes were relatively small (Seshappa and Bhimacher, 1954). Similarly, although female *C. abbreviatus* (to 348 mm TL) from Jiaozhua Bay, China, were larger than males (to 321 mm TL), average total lengths at age between the sexes were not significantly different (Zhu and Ma, 1992). Females of *C. bilineatus* and *C. arel* were also reported to be larger than males sampled from the same populations (Hoda and Khalil, 1995), whereas sizes for adult female (83–173 mm TL) and male (84–168 mm TL) *C. macrostomus* were found to be similar (Victor, 1981). Female *C. canariensis* also grow larger than males (Chauvet, 1972). For *C. semilaevis* inhabiting the Bohai Sea, China (Meng and Ren, 1988), quite a different situation exists. In this species, females attain lengths (to 638 mm TL) slightly more than twice those reached by males (to 312 mm TL). In other estuarine flatfish, such as the hogchoker, which occurs throughout much of the geographic range of the blackcheek tonguefish, females grow to larger sizes than do males from the same population (Koski, 1978). For most species of the Pleuronectidae, females also typically grow larger and have both a later age and larger size at maturity than do males (Cooper[4]).

Back-calculated lengths-at-age for blackcheek tonguefishes were consistently less than observed lengths-at-age for all age groups combined, which may be attributed to Lee's phenomenon. The principal cause of Lee's phenomenon in unexploited fish populations, such as that of blackcheek tonguefish inhabiting Chesapeake Bay, is that faster growing fish tend to mature and die earlier than do smaller members of the same year class (Gerking, 1957; Ricker, 1975). When a larger proportion of older fish die, the result is a smaller estimated size for fish at younger ages than the true average size at the age in question. Since blackcheek tonguefishes are not harvested commercially or recreationally within the Bay, the presence of Lee's phenomenon in the back-calculation estimates may be due to higher mortality of larger individuals within an age class, or possibly this finding may reflect the fact that larger fish move out of the Bay system and onto the nearby shelf region. The ages of blackcheek tonguefishes occurring on the continental shelf throughout the species' range are unknown. No offshore samples of blackcheek tonguefishes were collected during this study, and it is unknown if any of these fish are older than those occurring in Chesapeake Bay.

Although female blackcheek tonguefishes captured in Chesapeake Bay grew at a slightly faster rate than did males, observed differences in back-calculated lengths between male and female blackcheek tonguefishes beyond age 4 were not statistically significantly different. However, our sample sizes for older fish were small and interpretation of data for this oldest age class is limited. In other cynoglossids, such as Malabar sole, faster growth has also been observed in females compared with that for males (Seshappa and Bhimachar, 1954). Rajaguru (1992) found that female *C. arel* grew faster than males, but no significant differences in growth patterns were found between female and male *C. lida*. After their first year, female hogchokers in the Hudson River also grew faster than males (Koski, 1978). In some species of the Soleidae, such as the Agulhas sole (*Austroglossus pectoralis*) occurring off South Africa (Zoutendyk, 1974) and *Solea solea* in Spanish waters (Ramos, 1982), females also have a faster growth rate than do males within the same populations. A faster growth rate for females compared with that of males has also been reported in a variety of other flatfish species (Chen et al., 1992; Santos, 1994).

Estimates of the growth parameter *K* (Table 5) for blackcheek tonguefish are relatively high, indicating that these fish reach their asymptotic length relatively rapidly (Francis, 1996). Few estimates of *K*-values are available for other tonguefishes, but for those species studied, growth rates are relatively high. Where data are available, all, except two species, have higher growth coefficients reported for females. In *C. arel*, *K*-values were 0.315 for females and 0.238 for males, and in *C. lida* *K*-values of 0.233

[4] Cooper, J. A. 1998. National Marine Fisheries Service, National Systematics Laboratory, Washington, DC 20560. Personal commun.

for females and 0.223 for males were reported (Rajaguru, 1992). For *C. abbreviatus* (Zhu and Ma, 1992), *K*-values were 0.395 for females and 0.344 for males. In two of the largest species in the family, *C. semilaevis* and *C. canariensis,* the estimated *K*-values were higher for males compared with those for females. In *C. semilaevis*, *K*-value for females was 0.264, and that of males was 0.352 (Meng and Ren, 1988). For female *C. senegalensis* the *K*-value was 0.32 compared with 0.36 for males (Chauvet, 1972).

Table 5

Comparision of von Bertalanffy parameters of selected Pleuronectiformes occuring in temperate estuaries of the western North Atlantic.

Species	Parameters	Source
Paralichthys dentatus (♀ ♂)	K: 0.215 L_∞: 859 mm t_0: –0.690	Desfosse, 1995
Paralichthys lethostigma (♀)	K: 0.235 L_∞: 760 mm t_0: 0.570	Miller et al., 1991
Scophthalmus aquosus (♀)	K: 0.272 L_∞: 383 mm t_0: 0.418	Miller et al., 1991
Pseudopleuronectes americanus (♀)	K: 0.217 L_∞: 375.8 mm t_0: 0.730	Miller et al., 1991
Symphurus plagiusa (♀ ♂)	K: 0.308 L_∞: 192.4 mm t_0: –0.832	Terwilliger, 1996
Trinectes maculatus (♀)	K: 0.195 L_∞: 209.5 mm t_0: –0.353	Miller et al., 1991

In Chesapeake Bay, blackcheek tonguefishes achieve most of their growth in length during their first year. Males and females attained up to 50% of their total growth in length by the end of their first year, and up to 72% of their total growth by the end of their second year. Such rapid first-year growth does not appear to be unusual among members of the Cynoglossidae. For example, male *C. arel* grew between 180–194 mm TL, and females from 201–210 mm TL, during their first year (Rajaguru, 1992), which represented up to 58% and 51% of their total growth in length (333 and 393 mm, respectively). Similar to the pattern observed in blackcheek tonguefish, second-year growth in this species was estimated to be only 18% and 21% of the total growth, respectively, for males and females. In *C. lida*, males (151–154 mm TL) and females (153–156 mm TL) also reached fairly large sizes during their first year of life, with first-year growth for males and females ranging between 69 and 71% of the total growth in length (216 and 218 mm, respectively), compared with second-year growth values of only 13–14% of the total length (Rajaguru, 1992). *Cynoglossus macrolepidotus* also has a high growth rate during its first year, reaching a length of about 160 mm TL, and like the preceding species, during the second and subsequent years there occurs a marked reduction (only 10–30 mm increase/yr) in growth rate (Kutty, 1967). Likewise, in *C. abbreviatus* (Zhu and Ma, 1992), first-year growth is maximal for both sexes (males to 162 mm TL, females to 178 mm TL; representing 50% and 51% of total growth, respectively), whereas second-year growth in this species averages only about 16% or less of the total growth. This growth pattern was also apparent for *C. canariensis* where male and female fish, respectively, achieved 50% and 55% of their total growth in length during the first year, compared with second-year growth equalling only 14–15% of the total growth in length (Chauvet, 1972). In another large-size species, *C. semilaevis,* first-year growth is also rapid, with males reaching 141 mm TL at end of year one and females growing to 194 mm TL, values that represent 45% and 30% of the total growth in length achieved by this species (Meng and Ren, 1988). However, in contrast to other cynoglossid species examined thus far, growth in this species during the second year differs markedly between the sexes. For females, the average growth increment during the second year was greater than that of the first year (to 307 mm TL, 36% of total growth in length), whereas during this same time interval males averaged only about one-half of the growth increment attained during year one (to 204 mm TL, representing 20% of total growth). In the hogchoker, growth in length is also rapid; males and females achieve 56% and 44% of their total growth in length during the first year (Koski, 1978). By the end of their second year, hogchokers have reached on average 74% (males) and 63% (females) of their total growth in length.

The substantial reduction in growth rate beyond age 1 noted for blackcheek tonguefishes occurs at a time coincident with maturation (Terwilliger, 1996). Roff (1982) noted that, for fish in general, it is frequently observed that rate of growth decreases with

the onset of maturity. This slowing in somatic growth may reflect an allocation of energy to gonadal development, or may be a response to other physiological processes associated with maturation. Other cynoglossid species that have been aged also mature sexually at a relatively early age even in some of the larger-size species. Seshappa and Bhimachar (1954) reported that young Malabar soles (*C. semifasciatus*) grew to adult size within a year or less and that after maturation, growth slowed distinctly. After an initially high growth rate during their first year, there also occurred a marked reduction in the growth rate of *C. macrolepidotus* during their second year, at a time coincident with initiation of the spawning season (Kutty, 1967). Likewise, in other cynoglossids (*C. arel* and *C. lida*) occurring off India, growth during the first year is also rapid and this fast growth period is then followed by a considerable reduction in the growth rate during the next year when the fishes matured sexually (Rajaguru, 1992). In *C. arel*, for example, which reaches total lengths to 333 mm SL, males and females mature at sizes of about 217 mm TL and 225 mm TL, respectively, sizes reached by this species at the beginning of their second year of life. In *C. lida*, size at 50% maturity is 167 mm TL for males, and 179 mm TL for females. These represent sizes that are reached by the fish during the beginning of their second year of life. For *C. dubius* (Seshappa, 1976) minimum size at maturity was reported to be about 287 mm TL for females, a size that corresponded to fish approximately 2–3 years old. In *C. canariensis*, a species reaching total lengths of 486 mm (males) and 519 mm (females), maturity occurs at about 1.5 years when fish are about 300 mm TL (Chauvet, 1972).

Hoenig's and Royce's mortality estimates, based on the maximum known age of a species, indicate a relatively high instantaneous total mortality in the blackcheek tonguefish population inhabiting Chesapeake Bay (Table 6). Relatively few of the blackcheek tonguefishes within Chesapeake Bay are older than three years. The age structure observed in this population may, however, reflect the relatively short life span of this species (5+ years), or it could also reflect high mortality levels experienced by blackcheek tonguefishes in the Bay environment; undoubtedly it would also be influenced by the emigration of larger individuals from the Bay system.

Relatively short life spans may be typical of species of *Symphurus* and of the Cynoglossidae, in general. In fact, some dwarf species of tropical *Symphurus* reach maximum sizes of only 35–45 mm SL (Munroe, 1990, 1998) and probably live no more than a year. Age estimates based on growth marks interpreted from scales of tonguefishes occurring in coastal waters off India indicate that Malabar sole reach an age of only about 2+ years (Seshappa and Bhimachar, 1954). Based on studies of tonguefishes from the west coast of India, a life span of 3–4 years was reported by Seshappa (1978, 1981) for *C. lida* (size to 220 mm TL; most 140–189 mm TL) and *C. puncticeps* (to 209 mm TL; most 90–179 mm TL), whereas a life span of 6+ years (to 339 mm TL; most 160–299 mm TL) was reported for *C. bilineatus* from the same region. More recently, Rajaguru (1992) reported that *C. arel* and *C. lida* along the southeast coast of India have life spans just over 3 years. For *C. dubius* off India (to 414 mm TL), age estimates were 6+ years for most individuals, although some individuals reached 10 years (Seshappa, 1976). *Cynoglossus arel* off Taiwan (Lin, 1982) live to be at least 4 years. Kutty (1967) reported a maximum age of 6–7 years for *C. macrolepidotus* (to 330 mm TL). For *C. canariensis* (to 519 mm TL) off tropical West Africa, both sexes live to at least 8 years (Chauvet, 1972). For the temperate species, *C. abbreviatus*, from Jiaozhua Bay, China (Zhu and Ma, 1992), which is commercially exploited, females reach 8 years and males live to 7 years, and total mortality for this population was estimated to be very high (0.607). For

Table 6

Mortality estimates (Z) for various northwestern Atlantic Pleuronectiformes based on Hoenig's and Royce's equations. Values in parentheses reflect extrapolated mortality rates for a possible seventh age class of blackcheek tonguefish, *Symphurus plagiusa*, found in lower Chesapeake Bay and the inner continental shelf.

Species	Maximum age	Hoenig's equation	Royce's equation	Data source
Winter flounder (*P. americanus*)	14 years	0.32	0.33	Lux, 1973
Summer flounder (*P. dentatus*)	9 years	0.49	0.51	Desfosse, 1995
Windowpane (*S. aquosus*)	7 years	0.62	0.66	Moore, 1947
Southern flounder (*P. lethostigma*)	6 years	0.73	0.77	Music and Pafford, 1984
Hogchoker (*T. maculatus*)	6 years	0.73	0.77	Mansuetti and Pauly, 1956
Blackcheek tonguefish (*S. plagiusa*)	5 years (6 years)	0.87 (0.73)	0.92 (0.77)	Terwilliger, 1996

C. semilaevis from Chinese waters, a strong sexual dichotomy in longevity was apparent in the population studied; females reached 14 years (most 2–8 years), whereas males in this population attained a maximum age of only 5 years (Meng and Ren, 1988). By comparison, longevity estimates for a variety of other flatfishes occurring in temperate latitudes and from families other than the Cynoglossidae range from 6 to 30 years (Devold, 1942; Arora, 1951; Pitt, 1967; Lux and Nichy, 1969; Lux, 1970, 1973; Koski, 1978; Wada, 1970; Zoutendyk, 1974; Smith and Daiber, 1977).

As stated earlier, the population of *S. plagiusa* in Chesapeake Bay represents the northernmost location of a major population of this species (Munroe, 1998). In the western North Atlantic, variability in abiotic conditions increases from southern to northern latitudes (Parr, 1933; Miller et al., 1991). Abiotic variability also increases in environments located closer to the shoreline (Russell-Hunter, 1970; Miller et al., 1991). Fluctuations in abiotic factors, especially seasonal extremes of temperature during winter, may contribute to the high level of total instantaneous mortality measured for blackcheek tonguefishes within Chesapeake Bay. Bottom trawls conducted in this system during late winter and early spring of some years (1996, for example) catch numerous dead and moribund tonguefishes (Geer[5]), apparently due to stresses associated with extremely cold water temperatures (ca. 2°C. in 1996). More extreme winter temperatures and longer duration of cold temperatures may be a factor limiting the establishment of populations of blackcheek tonguefishes in more northern estuaries, where this species is known only by the occurrence of newly settled juveniles. In coastal estuaries throughout its U.S. geographic range, blackcheek tonguefishes appear to be sensitive to extreme winter temperatures, because winter mortalities have also been reported for this species in estuaries even as far south as those in Texas (McEachron et al., 1994). In addition to causing death outright, stresses associated with extreme winter temperatures may also render weakened tonguefishes easier prey to predators and thus further contribute to winter mortalities.

Mortality estimates for the population of blackcheek tonguefishes residing in Chesapeake Bay may also be inflated due to emigration of larger individuals out of the Bay and onto the nearby continental shelf. Hildebrand and Cable (1930) earlier had suggested that adult blackcheek tonguefishes in North Carolina estuaries undergo a seaward migration during May–August. An autumn emigration of blackcheek tonguefishes from Chesapeake Bay to the nearby shelf region just outside of the Bay may be reflected in the significantly larger catches (mean no./tow) of blackcheek tonguefishes reported (VIMS[6]) in this region during fall sampling (1987, 75.4/tow; 1988, 25.7/tow) compared with springtime catches (1987, 11.0/tow; 1988, 4.37/tow; 1989, 2.2/tow). Data supplied in Wenner and Sedberry (1989) also support the hypothesis that there is a seasonal migration of larger tonguefishes out of estuaries and onto the coastal shelf off South Carolina. They reported that this species was widespread throughout the survey area but noted that significant seasonal differences were apparent in the frequency of occurrence and abundance of *S. plagiusa* in coastal habitats. This species occurred less frequently during winter (48% of all tows; 566 individuals) than in spring (85% of tows; 1,460 individuals), summer (76% of tows; 798 individuals), or fall (94% of tows; 5962 individuals). Catches (mean no./tow) of this species were lowest in summer (8/tow) and winter (9/tow), higher in spring (21/tow), and highest during the fall (62/tow), when the largest fish (up to 210 mm TL) were taken. Although Wenner and Sedberry (and other studies) have reported that it is usually only larger-size blackcheek tonguefishes that are captured on the inner shelf region, no studies have verified any seasonal or spawning movements of blackcheek tonguefishes out of the estuaries, or the amount of exchange of individuals within populations between estuarine embayments and adjacent neritic habitats on the inner shelf. It is also unknown whether all larger individuals undergo an ontogenetic migration out of estuaries onto the nearby shelf; what portion of a population residing in estuaries moves out onto the shelf at any given age; what the estuarine residency time is for larger tonguefishes, especially in such larger and deeper estuaries as the Chesapeake Bay which may be utilized by larger tonguefishes for longer periods of time; or even if further exchange of individuals between these two environments occurs once an individual has emigrated beyond the estuarine boundary. Analysis of catch curve data (Fig. 10) may also lend insight on inflated mortality estimates. Although the bimodality of the catch curve data infers possible variability in year-class strength that invalidates its use for mortality estimations (Robson and Chapman, 1961; Everhart and Youngs, 1981), the data suggest that a seventh year class may exist, possibly on the nearby shelf region. If so, mortality estimates based on a maximum age of 5+ years

[5] Geer, P. J. 1996. VIMS, Department of Fisheries, Gloucester Point, VA 23062. Personal commun.

[6] VIMS, Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

would be inflated compared with those calculated for an older year class.

Sex ratio of tonguefishes sampled during this study deviated from 1:1 mostly due to large single-sex catches of females during the summer months in the lower Bay. In lower Chesapeake Bay, apparently some spatial separation of the sexes occurs (Terwilliger, 1996). Here, dense concentrations of female blackcheek tonguefishes were commonly found in the deeper areas, and fewer males were taken in the same trawls. Among sympatric species of pleuronectiforms, the hogchoker also reportedly displays bathymetric separation of the sexes in tributaries of Chesapeake Bay during the summer months prior to spawning (Mansuetti and Pauly, 1956), when females occupy grass beds and shoal regions, while males are surmised to occupy deeper areas within the estuary. This pattern of habitat segregation by adult hogchokers, however, was not evident in the study conducted by Koski (1978) in the Hudson River, although he noted that although the overall sex ratio for fishes examined did not differ from 1:1, some individual trawl catches were dominated by or consisted entirely of one sex. Significant differences in the sex ratios of catches of other tonguefishes have also been reported. Seshappa and Bhimachar (1955) noted that sex ratios of catches of Malabar sole during the spawning period were markedly different than those made during other times of the year and attributed these differences to differential behavior of the two sexes during their spawning migrations. Hoda and Khalil (1995) also reported skewed sex ratios (1.0:2.55 males to females) for catches of *Cynoglossus arel*, whereas those (1.16:1) for *C. bilineatus* were not significantly different from 1:1. A skewed ratio (1.56:1) favoring females over males was also found for *C. semilaevis* (Meng and Ren, 1988). Although some studies have inferred spatial differences in movements of the different sexes of cynoglossid tonguefishes based on fisheries catch data, it is difficult to draw any general conclusions from these data. Just as we lack reliable documentation concerning spatial movements for the two sexes of blackcheek tonguefish, directed studies providing the detailed information necessary for interpreting adult movements of any of these other cynoglossid species have yet to be performed.

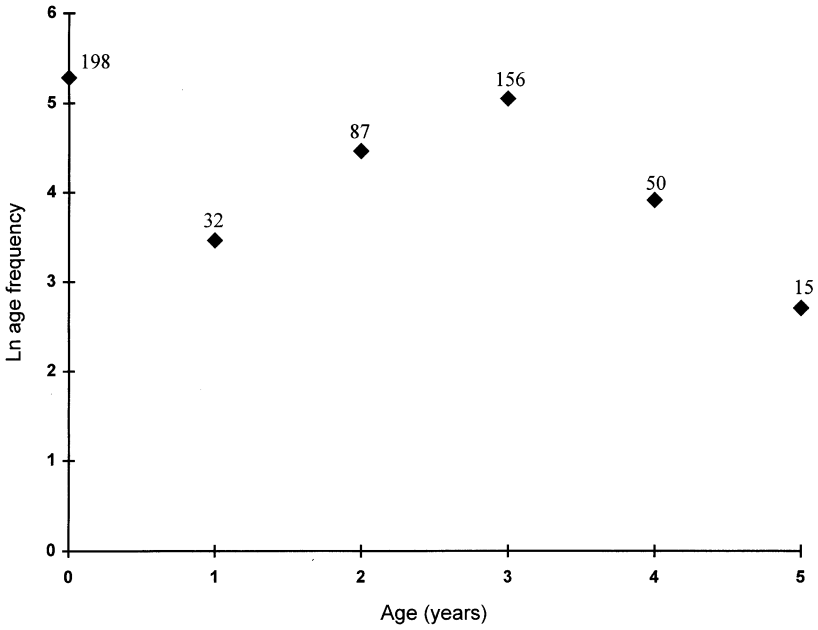

Figure 10

Catch curve for blackcheek tonguefish, *Symphurus plagiusa*, collected by otter trawl in lower Chesapeake Bay and major lower tributaries, 1993–95. Numbers above plot represent numbers at each age.

North temperate estuaries, such as Chesapeake Bay, are rigorous physical systems well known for environmental extremes in temperature, salinity, and dissolved oxygen, and for strong seasonal cycles of primary and secondary production. However, the extensive distribution within the Bay and its tributaries of shallow, soft bottom sediments presents considerable amounts of suitable habitat for flatfishes. Twelve species of flatfishes have been recorded from the Bay (Murdy et al., 1997). The unique geographical location of Chesapeake Bay at the northern end of a warm temperate and southern end of a cold temperate region (Briggs, 1974) may account for the occurrence within the Bay of diverse faunal components, which have either warm or cold water affinities. Among pleuronectiforms inhabiting Chesapeake Bay, for example, are six species representing five different families (Cynoglossidae, Achiridae, Paralichthyidae, Scophthalmidae, and Pleuronectidae). This assemblage includes representatives of families whose species occur primarily in cold temperate or boreal areas (Scophthalmidae, Pleuronectidae) or in warm temperate and tropical regions (Cynoglossidae, Achiridae, Paralichthyidae). Of the species occurring within Chesapeake Bay are blackcheek tonguefish, hogchoker, and smallmouth flounder,

Etropus microstomus (to ca. 159 mm TL), small-size species that are not commercially or recreationally exploited and ones that complete their life cycles within the Bay. Virtually nothing is known concerning age and growth of smallmouth flounder, especially within the Bay system; therefore further comparisons of its life history with those of sympatric flatfishes are limited. The flatfish fauna of the Bay also includes summer flounder (*Paralichthys dentatus*), southern flounder (*Paralichthys lethostigma*), windowpane (*Scophthalmus aquosus*), and winter flounder (*Pseudopleuronectes americanus*), species that do not necessarily complete their life cycles entirely within Chesapeake Bay and ones that are heavily exploited both commercially and recreationally. The remaining species of flatfishes recorded from the Bay are transient species that occur only irregularly within the Bay and will not be discussed further. The diversity in size and growth parameters represented among those flatfishes occurring in Chesapeake Bay which have been studied provides an interesting opportunity for investigating comparative life histories of sympatric members of an estuarine benthic fish assemblage with somewhat similar lifestyles (Table 5).

Few published age-growth studies exist for noncommercially exploited flatfishes, especially for those species occurring in temperate estuaries of the western North Atlantic. Von Bertalanffy growth parameters for species other than blackcheek tonguefish were taken from data found in the literature (Miller et al., 1991; Desfosse, 1995). These data reveal that among this assemblage, blackcheek tonguefish have the highest value for growth parameter *K* (Table 5), and therefore reach asymptotic length faster than sympatric counterparts (Francis, 1996). Of sympatric flatfishes occurring in Chesapeake Bay, only hogchokers display growth parameters and maturation schedules (some males mature at end of first year, most of both sexes mature by age 2; Koski, 1978) similar to those observed for blackcheek tonguefish. In contrast, summer and southern flounders mature at ages 2–3, windowpane flounders mature at ages 3 or 4, and winter flounders mature at ages 2–5. Later age at maturation in these species reflects a different life history pattern, and one that allows for energy allocation favoring increased somatic growth during several years prior to the onset of maturation. Because these other species mature at later ages than do blackcheek tonguefish and hogchoker, growth in length for these fishes would be relatively rapid over the course of several years during the early part of their lives (Fig. 11).

Estimates of asymptotic length, reflecting average maximum length attained by a species, also varies considerably among members of this assemblage. Asymptotic lengths for summer flounder (859 mm TL) and southern flounder (to 760 mm) greatly exceed those for blackcheek tonguefish and hogchoker (192 and 210 mm, respectively). In fact, these fishes grow more during their first year than do blackcheek tonguefish and hogchokers in a lifetime. Windowpane and winter flounder (383 and 376 mm, respectively) attain asymptotic lengths intermediate to these other two groups of sympatrically occurring estuarine flatfishes.

Estimates of instantaneous total mortality based on blackcheek tonguefishes caught within Chesapeake Bay during this study are also relatively higher when compared with those for most other estuarine dependent species of northwestern Atlantic Pleuronectiformes (Table 6). In this comparison, blackcheek tonguefish are among the shortest-lived species and therefore have one of the higher rates of instantaneous total mortality. Relatively few individuals within Chesapeake Bay are older than three years. Extrapolating mortality rates for a possible seventh year class (age 6+), which may be found on the inner shelf region, provides an instantaneous total mortality estimate comparable to those for hogchokers and southern flounder caught in Chesapeake Bay.

Blackcheek tonguefish exhibit the youngest age at first maturity, the highest growth coefficient, the youngest known maximum age, and the smallest asymptotic length when compared with sympatric pleuronectiforms from Chesapeake Bay. Blackcheek tonguefish exhibit rapid growth until maturity, after which growth rate declines markedly. Munroe (1990, 1998) indicated that eight dwarf species of *Symphurus* reach sexual maturity between 28 and 45 mm SL. Small size and presumably early age at maturation may be characteristic of species in this genus (Munroe, 1988); even *S. jenynsi*, the largest species in the genus (reaching ca. 350 mm TL), matures at a relatively small size (about 132 mm TL). More ageing studies on fishes of this genus are required to test this hypothesis. Other cynoglossid flatfishes, although they attain a relatively large size before reaching sexual maturity, are only 1 or 2 yr old when first maturing. According to available data, it is quite possible then that tonguefishes in general have an age dependent maturity schedule. Roff (1982) indicated that age, and not size, would appear to be most important in fish species that mature early. Data for tonguefishes support that finding.

When compared with estimates for sympatric flatfishes, blackcheek tonguefish caught during this study exhibit the highest rates of instantaneous total mortality. Other species inhabiting the Bay system also mature at larger sizes, have larger asymptotic lengths, and slower growth rates. Interesting

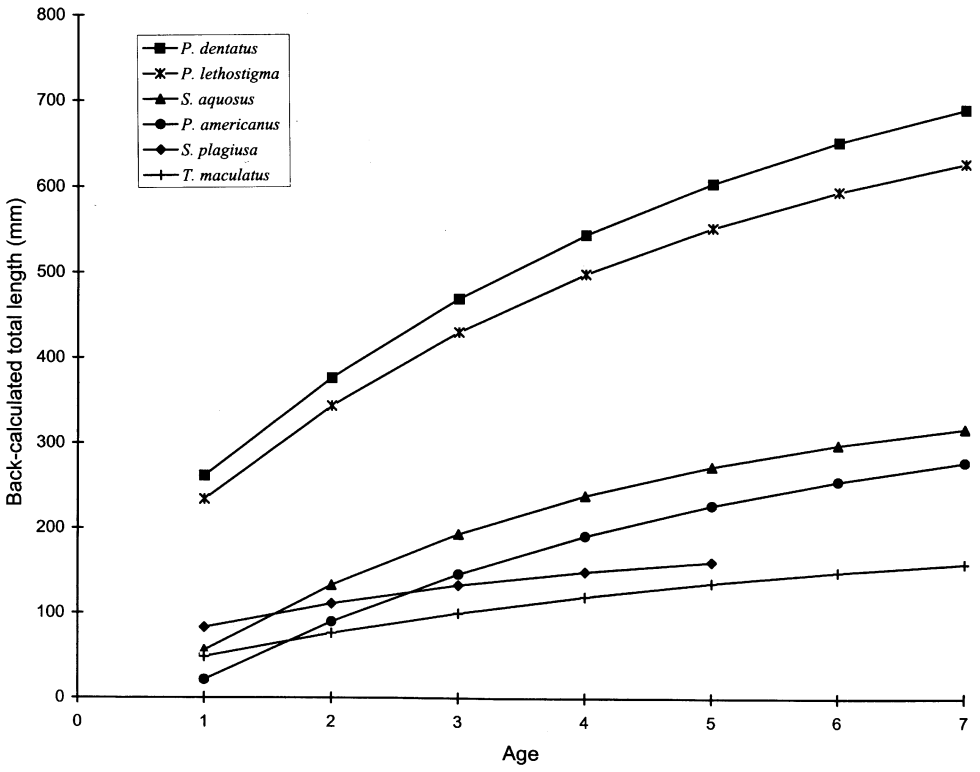

Figure 11

Von Bertalanffy growth curves for selected Pleuronectiformes occurring in western North Atlantic temperate estuaries. Values for species other than *Symphurus plagiusa* were derived from the literature.

to note, it is only the smallest-size and shortest-lived flatfishes (*S. plagiusa*, *T. maculatus*, and probably *E. microstomus*) that complete their life cycles within Chesapeake Bay. Under an environmental regime with a large component of unpredictable, nonselective mortality, an organism is hypothesized to allocate a larger portion of its resources to reproductive activities (Adams, 1980). Life history parameters, such as rapid growth, small body size, early age at maturity and relatively short life span, characteristics featured in these small-size flatfishes completing their life cycles within Chesapeake Bay, are consistent with those observed for other fish species that survive in and successfully exploit seasonally dynamic and highly unpredictable environments.

Acknowledgments

This study represents part of a M.A. thesis (by Mark R. Terwilliger) at the School of Marine Science, Virginia Institute of Marine Science, College of William and Mary. We thank Joy Dameron, Deane Estes, Eric Farrar, Pat Geer, Paul Gerdes, Dave Hata, Mike Land, Todd Mathes, Dee Seaver, Mike Seebo, and Chandell Terwilliger of VIMS for assisting in field collections and for providing data and specimens. We extend our appreciation to Herb Austin for allowing us access to sources of unpublished data archived in the VIMS Fisheries Department. This study benefited from financial support arranged by Herb Austin, Jack Musick, Gene Burreson, and Joe Loesch (VIMS). Additional financial support was provided by the VIMS minigrant committee, the student conference fund of the College of William and Mary, and by the American Institute of Fisheries Research Biologists' student conference fund. Chandell Terwilliger provided moral support throughout the course of the study. Pat Geer, Dave Hata, Steve Bobko (ORST), and Mike Murphy (FL DEP) provided valuable insight on statistical analyses. A special thanks to Pat Geer for his help with trawl survey data analysis and manipulation. Tom Sminkey (FL DEP) provided useful instruction on use of the Biosonics Optical Pattern Recognition System, and Dave Harshany (FL DEP) helped with image production

using Optimas software. Martha Nizinski (VIMS) assisted with figure preparation. Sandra Raredon, Division of Fisheries, Smithsonian Institution, provided assistance with manuscript translation. Roy Crabtree, Tom Sminkey (FL DEP), Kathy Lang (NMFS, Woods Hole), Bruce Collette (NMFS Systematics Laboratory), and three anonymous reviewers critically reviewed earlier drafts of the manuscript.

Literature cited

Adams, P. B.
1980. Life history patterns in marine fishes and their consequences for fisheries management. Fish. Bull. 78:1–12.

Arora, H. L.
1951. An investigation of the California sand dab, *Citharichthys sordidus* (Girard). Calif. Fish Game 37(1):3–42.

Bagenal, T. B., and F. W. Tesch.
1978. Age and growth. *In* T. B. Bagenal (ed.), Methods for assessment of fish production in fresh waters, 3rd ed., p. 101–136. Blackwell Scientific Publications, Oxford.

Barbieri, L. R.
1993. Life history, population dynamics and yield-per-recruit modeling of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay area. Unpubl. Ph.D. diss., College of William and Mary, Williamsburg, VA, 140 p.

Biosonics, Inc.
1987. Optical Pattern Recognition System data acquisition program manual, version 1.08. Biosonics, Inc., Seattle, WA, 112 p.

Bonzek, C. F., P. J. Geer, J. A. Colvocoresses, and R. E. Harris Jr.
1993. Juvenile finfish and blue crab stock assessment program, bottom trawl survey, annual data summary. Annual data summary report series, vol. 1992. Special Scientific Report 124, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA, 217 p.

Briggs, J. C.
1974. Marine zoogeography. McGraw-Hill Book Co., New York, NY, 475 p.

Cerrato, R. M.
1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Can. J. Fish. Aquat. Sci. 47:1416–1426.

Chauvet, C.
1972. Croissance et détermination de l'âge par lecture d'ecailles d'un poisson plat de Côte d'Ivoire *Cynoglossus canariensis* (Steind. 1882). Doc. Scient. Cent. Rech. Oceanogr. Abidjan 3:1–18.

Chen, D., C. Liu, and S. Dao.
1992. The biology of flatfish (Pleuronectidae) in the coastal waters of China. Neth. J. Sea. Res. 29:25–33.

Chittenden, M. E., Jr., and S. D. McEachran.
1976. Composition, ecology, and dynamics of demersal fish communities on the northwestern Gulf of Mexico continental shelf, with a similar synopsis for the entire Gulf. Texas A&M University, TAMU-SG-76-208, 104 p.

Dawson, C. E.
1965. Length-weight relationships of some Gulf of Mexico fishes. Trans. Am. Fish. Soc. 94(3):279–280.

Desfosse, J. C.
1995. Movements and ecology of summer flounder, *Paralichthys dentatus*, tagged in the southern mid-Atlantic bight. Unpubl. Ph.D. diss., College of William and Mary, Williamsburg, VA, 187 p.

Devold, F.
1942. Plaice investigations in Norwegian waters. Rep. Norw. Fish. Mar. Invest. VII(3), 83 p.

Everhart, W. H., and W. D. Youngs.
1981. Principles of fishery science, 2nd ed. Cornell Univ. Press, Ithaca, New York, NY, 349 p.

Francis, R. I. C. C.
1996. Do herring grow faster than orange roughy? Fish. Bull. 94:783–786.

Geer, P. J., H. M. Austin, and C. F. Bonzek.
1997. Juvenile fish and blue crab stock assessment program bottom trawl survey annual data summary report. Annual data summary report series, vol. 1996. Special Scientific Report 124, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA, 275 p.

Geer, P. J., J. A. Colvocoresses, H. M. Austin, and C. Bonzek.
1993. Estimation of relative abundance of recreationally important finfish in the Virginia portion of Chesapeake Bay: annual progress report. U.S. Fish and Wildlife Service Sportfish Restoration Project F104R2, College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, VA, 105 p.

Gerking, S. D.
1957. Evidence of ageing in natural populations of fishes. Gerontologia 1:287–305.

Ginsburg, I.
1951. Western Atlantic tonguefishes with descriptions of six new species. Zoologica (NY) 36:185–201.

Heidinger, R. C., and K. Clodfelter.
1987. Validity of the otolith for determining age and growth of the walleye, striped bass, and smallmouth bass in power plant cooling ponds. *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth in fish, p. 241–251. Iowa State Univ. Press, Ames, IA.

Hildebrand, S. F., and L. E. Cable.
1930. Development and life history of fourteen teleostean fishes at Beaufort, North Carolina. Bull. U.S. Bur. Fish. 43:383–488.

Hildebrand, S. F., and W. C. Schroeder.
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43:1–366.

Hoda, S. M. S., and B. Khalil.
1995. Observations on the biology of *Cynoglossus bilineatus* (Lacep.) and *C. Arel* (Bl. & Schn.) from the Karachi-Sindh coast. *In* M. F. Thompson and N. M. Tirmizi (eds.), The Arabian Sea: living marine resources and the environment, p. 309–330. Vanguard Books Ltd., Lahore, Pakistan.

Hoenig, J. M.
1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82:898–902.

Jearld, A., Jr.
1983. Age determination. *In* L. A. Nielsen and D. L. Johnson (eds.), Fisheries techniques, p. 301–324. Am. Fish. Soc., Bethesda, MD.

Jorgenson, S. C., and G. L. Miller.
1968. Length relations of some marine fishes from coastal Georgia. U.S. Fish Wildl. Serv. SSR-Fisheries, No. 575, 16 p.

Kimura, D. K.
1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77:765–775.

Koski, R. T.
1978. Age, growth, and maturity of the hogchoker, *Trinectes maculatus*, in the Hudson River, New York. Trans. Am. Fish. Soc. 107:449–453.

Kutty, M. K.
1967. Observations on the growth and mortality of the large scaled tonguefish *Cynoglossus macrolepidotus* (Bleeker). Proc. Natl. Inst. Sci. India 33:94–110.
Lagler, K. F.
1956. Freshwater fishery biology, 2nd ed. W.C. Brown Co. Publ., Dubuque, IA, 421 p.
Lin, M.-C.
1982. Age and growth of north Taiwan tongue sole *Cynoglossus arel*. Bull. Taiwan Fish. Res. Inst. 34:91–99.
Lux, F. E.
1970. Note on growth of American plaice, *Hippoglossoides platessoides* (Fabr.) in ICNAF Subarea 5. Int. Comm. Northwest Atl. Fish. Spec. Publ. 7:5–7.
1973. Age and growth of the winter flounder, *Pseudopleuronectes americanus*, on Georges Bank. Fish. Bull. 71:505–512.
Lux, F. E., and F. E. Nichy.
1969. Growth of yellowtail flounder, *Limanda ferruginea* (Storer), on three New England fishing grounds. Int. Comm. Northwest Atl. Fish. Res. Bull. 6:5–25.
Mansuetti, R., and R. Pauly.
1956. Age and growth of the northern hogchoker, *Trinectes maculatus*, in the Patuxent River, Maryland. Copeia 1956:60–62.
McEachron, L. W., G. C. Matlock, C. E. Bryan, P. Unger, R. J. Cody, and J. H. Martin.
1994. Winter mass mortality of animals in Texas bays. Northeast Gulf Sci. 13(2):121–138.
Meng, T., and S. Ren.
1988. Age and growth of *Cynoglossus semilaevis* Günther in the Bohai Sea. Mar. Fish. Res. (Shandong) 9:173–183. [In Chinese, with English abstract.]
Menon, A. G. K.
1977. A systematic monograph of the tongue soles of the genus *Cynoglossus* Hamilton- Buchanan (Pisces: Cynoglossidae). Smithson. Contrib. Zool. 238:1–129.
Miller, J. M., J. S. Burke, and G. R. Fitzhugh.
1991. Early life history patterns of Atlantic North American flatfish: Likely (and unlikely) factors controlling recruitment. Neth. J. Sea. Res. 27:261–275.
Moe, M. A., Jr., and G. T. Martin.
1965. Fishes taken in monthly trawl samples offshore of Pinellas County, Florida, with new additions to the fish fauna of the Tampa Bay area. Tulane Stud. Zool. 12:129–151.
Moore, E.
1947. Studies on the marine resources of southern New England. 6. The sand flounder, *Lophopsetta aquosa* (Mitchill): a general study of the species with emphasis on age determination by means of scales and otoliths. Bull. Bingham Oceanogr. Coll. 11:1–79.
Munroe, T. A.
1990. Eastern Atlantic tonguefishes (*Symphurus*: Cynoglossidae: Pleuronectiformes), with descriptions of two new species. Bull. Mar. Sci. 47:464–515.
1998. Systematics and ecology of tonguefishes of the genus *Symphurus* (Cynoglossidae: Pleuronectiformes) from the western Atlantic Ocean. Fish. Bull. 96:1–182.
Murdy, E. O., R. S. Birdsong, and J. A. Musick.
1997. Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington, DC, 324 p.
Music, J. L., and J. M. Pafford.
1984. Population dynamics and life history aspects of major marine sportfishes in Georgia's coastal waters. Georgia Dep. Nat. Res., Coast. Res. Div., Contr. Ser. 38:1–382.
Olney, J. E., and G. C. Grant.
1976. Early planktonic larvae of the blackcheek tonguefish, *Symphurus plagiusa* (Pisces: Cynoglossidae), in the lower Chesapeake Bay. Ches. Sci. 17:229–237.
Parr, A. E.
1933. A geographic-ecological analysis of the seasonal changes in temperature conditions in shallow water along the Atlantic coast of the United States. Bull. Bingham Oceanogr. Lab. 4:1–90.
Pitt, T. K.
1967. Age and growth of American plaice (*Hippoglossoides platessoides*) in the Newfoundland area of the northwest Atlantic. J. Fish. Res. Board Can. 24:1077–1099.
Prather, E. E.
1967. The accuracy of the scale method in determining the ages of largemouth bass and bluegills. Proc. Ann. Conf. Southeast. Assoc. Game Fish Commission. 20:483–486.
Qasim, S. Z.
1973. Some implications of the problem of age and growth in marine fishes from the Indian waters. Indian J. Fish. 20(2):351–371.
Rajaguru, A.
1992. Biology of two co-occurring tonguefishes, *Cynoglossus arel* and *C. lida* (Pleuronectiformes: Cynoglossidae), from Indian waters. Fish. Bull. 90:328–367.
Ramanathan, N., P. Vijaya, V. Ramaiyan, and R. Natarajan.
1980. On the biology of the large scaled tongue sole *Cynoglossus macrolepidotus* (Bleeker). Indian J. Fish. 24:83–89.
Ramos, J.
1982. Estudio de la edad y crecimiento del lenguado, *Solea solea* (Linneo, 1758) (Pisces: Soleidae). Invest. Pesq. 46(1):15–28.
Reichert, M. J. M., and H. W. van der Veer.
1991. Settlement, abundance, growth, and mortality of juvenile flatfish in a subtropical tidal estuary (Georgia, U.S.A.). Neth. J. Sea. Res. 27:375–391.
Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Department of the Environment, Fisheries and Marine Service, Fish. Res. Board Can. Bull. 191, Ottawa, Canada, 400 p.
Robson, D. S., and D. G. Chapman.
1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181–189.
Roff, D. A.
1982. Reproductive strategies in flatfish: a first synthesis. Can. J. Fish. Aquat. Sci. 39:1686– 1698.
Royce, W. F.
1972. Introduction to the fishery sciences. Academic Press, New York, NY, 351 p.
Russell-Hunter, W. D.
1970. Aquatic productivity. The Macmillan Co., London, 306 p.
Saila, S. B., C. W. Recksieck, and M. H. Prager.
1988. Basic fishery science programs. Elsevier, Amsterdam, 230 p.
Santos, P. T.
1994. Growth and reproduction of the population of the four-spot megrim (*Lepidorhombus boscii* Risso) off the Portuguese coast. Neth. J. Sea. Res. 32:379– 383.
Seshappa, G.
1976. On the fishery and biology of the large tongue-sole, *Cynoglossus dubius* Day, at Calicut, Kerala. Indian J. Fish. 21:345–356.
1978. Report on a collection of tongue soles (*Cynoglossus* sp.) from Moplah Bay with a description of *C. lida* (Bleeker). Indian J. Fish. 23:160–173.

1981. Observations on the size distribution and the occurrence of growth rings in the scales of three species of *Cynoglossus* at Calicut. Indian J. Fish. 25:188–196.

Seshappa, G., and B. S. Bhimachar.

1954. Studies on the age and growth of the Malabar sole, *Cynoglossus semifasciatus* Day. Indian J. Fish. 1(1):145–162.

1955. Studies on the fishery and biology of the Malabar sole, *Cynoglossus semifasciatus* Day. Indian J. Fish. 2(1):180–230.

Seshappa, G., and B. K. Chakrapani.

1984. A scalimetric comparison of the malabar sole *Cynoglossus semifasciatus* Day from different centres of the west coast. Indian J. Fish. 31:82–89.

Shealy, M. H., Jr., J. V. Miglarese, and E. B. Joseph.

1974. Bottom fishes of South Carolina estuaries—Relative abundance, seasonal distribution, and length frequency relationships. Tech. Rep. 6, South Carolina Marine Resource Center, Charleston, SC, 189 p.

Smith, R. W., and F. C. Daiber.

1977. Biology of the summer flounder, *Paralichthys dentatus*, in Delaware Bay. Fish. Bull. 75:823–830.

Spurr, A. R.

1969. A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. 26:31–43.

Stickney, R. R.

1976. Food habits of Georgia estuarine fishes II. *Symphurus plagiusa* (Pleuronectiformes: Cynoglossidae). Trans. Am. Fish. Soc. 105:202–207.

Terwilliger, M. R.

1996. Age, growth, and reproductive biology of the blackcheek tonguefish, *Symphurus plagiusa* (Cynoglossidae: Pleuronectiformes), in Chesapeake Bay, Virginia. M.A. thesis, The College of William and Mary, Williamsburg, VA, 116 p.

Toepfer, C. S., and J. W. Fleeger.

1995. Diet of juvenile fishes *Citharichthys spilopterus*, *Symphurus plagiusa*, and *Gobionellus boleosoma*. Bull. Mar. Sci. 56(1):238–249.

Topp, R. W., and F. H. Hoff Jr.

1972. Flatfishes (Pleuronectiformes). Fla. Dep. Nat. Resour., St. Petersburg. Mem. Hourglass Cruises 4:1–135.

Vaughan, D. S., and M. L. Burton.

1994. Estimation of von Bertalanffy growth parameters in the presence of size- selective mortality: a simulated example with red grouper. Trans. Am. Fish. Soc. 123:1–8.

Victor, A. C. C.

1981. Length-weight relationship in the Malabar sole, *Cynoglossus macrostomus* Norman. Indian J. Fish. 25:259–262.

Wada, K.

1970. Studies on the population biology of the flatfish, *Limanda herzensteini* Jordan et Snyder, in Nigata Region. Bull. Jpn. Sea Reg. Fish. Res. Lab. 22:31–43.

Wenner, C. A., and G. R. Sedberry.

1989. Species composition, distribution, and relative abundance of fishes in the coastal habitat off the southeastern United States. NOAA Tech. Rep. NMFS-SSRF 79, 49 p.

White, M. L., and M. E. Chittenden Jr.

1977. Age determination, reproduction, and population dynamics of the Atlantic croaker, *Micropogonias undulatus*. Fish. Bull. 75:109–123.

Zhu, X., and D. Ma.

1992. Studies on age, growth, and age class structures of the tonguefish, *Cynoglossus abbreviatus* (Day) in the Jiaozhou Bay waters. Mar. Sci. (Beijing) 1:49–53. [In Chinese, with English abstract.]

Zoutendyk, P.

1974. The biology of the Agulhas sole, *Austroglossus pectoralis*. Part-2: Age and growth. Trans. R. Soc. So. Afr. 41(1): 33–41.